

Fallow deer polyandry is related to fertilization insurance

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Abstract Polyandry is widespread, but its adaptive significance is not fully understood. The hypotheses used to explain its persistence have rarely been tested in the wild and particularly for large, long-lived mammals. We investigated polyandry in fallow deer, using female mating and reproduction data gathered over 10 years. Females of this species produce a single offspring (monotocous) and can live to 23 years old. Overall, polyandry was evident in 12 % of females and the long-term, consistent proportion of polyandrous females observed, suggests that monandry and polyandry represent alternative mating strategies. Females were more likely to be polyandrous when their first mate had previously achieved high numbers of matings during the rut or was relatively old. However, polyandry was not related to the following factors: female age, the stage of the rut, the dominance ranks of mates, or the number of daily matings

achieved by males. Polyandrous and monandrous multiple-mating females were not more likely than single-mating females to be observed with an offspring during the following year, and there were no significant differences in offspring size between these females. These results provide support for a fertility insurance hypothesis, with females remating if fertilization from the first mating was uncertain due to possible sperm depletion. The potential for different female mating strategies among large, polygynous mammals has generally been overlooked. Our findings highlight the complexity of female reproductive strategies and the possible trade-offs between fertilization success, preferences for high-quality males, and potential costs of polyandry, particularly for monotocous species.

Keywords Female mate choice · Female mating strategy · Good genes · Offspring quality · Sexual selection · Ungulates

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Introduction

Polyandry occurs when females mate with more than one male during a fertile period (Andersson 1994). Its prevalence can have important evolutionary consequences, for example, in terms of sexual selection and maintaining population genetic diversity (Hosken and Stockley 2003; Collet et al. 2012). Despite considerable research, the adaptive significance of polyandry for female fitness is still subject to debate (Firman and Simmons 2011). Mating is costly in terms of increased predation risk and the energy and time spent searching for mates, selecting mates, and copulating (Byers et al. 2005). Copulations can also result in physical injury and sexually transmitted diseases (Daly 1978). Several hypotheses have been proposed to explain why polyandry persists (Yasui 1998; Jennions and Petrie 2000; Hosken and Stockley 2003), but they have rarely been tested in wild populations and particularly in large, long-lived mammals, in which females give birth to single offspring (monotocous; Wolff and Macdonald 2004).

The potential benefits of polyandry can be classified as “material” or “genetic,” but these are also not mutually exclusive (Hosken and Stockley 2003; Slatyer et al. 2012). Material benefits include boosting fertility/fecundity (Gibson and Jewell 1982) and avoidance of male infanticide (Wolff and Macdonald 2004) or physical harm that can occur when trying to resist mating (i.e., convenience polyandry; Huchard et al. 2012). Genetic benefits of polyandry can result from precopulatory (i.e., female choice for a better mate than the previous one; Jennions and Petrie 2000) or postcopulatory (i.e., sperm competition or cryptic female choice; Firman and Simmons 2011) mechanisms (Pischedda and Rice 2012). These benefits include the selection of mates with good and/or compatible genes (Jennions and Petrie 2000; Slatyer et al. 2012) and increased offspring genetic diversity (Tregenza and Wedell 2002). Indeed, polyandry could result in increased individual offspring heterozygosity in both monotocous and polytocous species by allowing females to choose less closely related males through precopulatory or postcopulatory mate selection (Tregenza and Wedell 2002; Bergeron et al. 2011). Alternatively, if a species is polytocous, females could increase litter genetic diversity by selecting several fathers for their offspring (Cornell and Tregenza 2007). As a result of these genetic benefits, polyandrous females may have greater offspring survival than monandrous females (Madsen et al. 1992; Fedorka and Mousseau 2002; Fisher et al. 2006). Females may mate once (monandrous single mating) or several times either with the same male (monandrous multiple mating) or with different males (polyandrous) during a given fertile period. Both monandrous multiple-mating females and polyandrous females could benefit from increased fertility/fecundity, whereas other benefits (e.g., good genes or offspring heterozygosity) apply to polyandrous females only (Wolff and Macdonald 2004; Slatyer et al. 2012).

Until recently, studies of ungulates (with some notable exceptions) tended to focus on male mating strategies and/or female maternal investment in offspring, while often ignoring female mating strategies (Endo and Doi 2002; Carling et al. 2003; Bebié and McElligott 2006; Bro-Jørgensen 2007, 2011; Vanpé et al. 2009; Bowyer et al. 2011). Opinions on ungulate female choice are still divided because males often try to restrict female movements and thereby might constrain female choice (Clutton-Brock and McAuliffe 2009; Bro-Jørgensen 2011), but nevertheless, there is strong evidence for ungulate female mate choice, including in fallow deer (Komers et al. 1999; Bro-Jørgensen 2002; Byers and Waits 2006; Bowyer et al. 2011; Farrell et al. 2011; Dunn et al. 2012). In addition, reports of polyandry in cervids are very rare (Endo and Doi 2002; Vanpé et al. 2009). We investigated polyandry in fallow deer (*Dama dama*), a highly polygynous, strongly size-dimorphic, and long-lived species (Farrell 2001; McElligott et al. 2001, 2002). We used female mating and reproduction data gathered over 10 years in a free-ranging park population,

in order to decipher the potential benefits that females obtain from polyandry.

Female fallow deer reach sexual maturity at 18 months, usually produce a single fawn per year, and can reproduce until 23 years old (Langbein and Putman 1992; Birgersson 1998; this study). Matings happen during the rut in October (northern hemisphere) and fawns are born during the following June (Langbein and Putman 1992; Lord 2006). Older multiparous females (>2 years old) mate both earlier in the rut and with older and higher-ranking males, compared to yearling, primiparous females (Farrell et al. 2011). When in estrus, most females mate once (Farrell 2001; Harty 2002; Say et al. 2003). However, each year in our study population, a consistent proportion (on average, 14.6 %) of females mate multiple times (range, 2–6) with the same or different males (Farrell 2001). Sneaky or coercive matings are very rare (Farrell 2001; Harty 2002), estrous females actively avoid young males (Komers et al. 1999), and as in other species, such as pronghorn (*Antilocapra americana*), females visit many mature males before mating (Harty 2002; Byers et al. 2005). Therefore, fallow deer show evidence for female-initiated polyandry, as opposed to male-initiated polyandry (e.g., “convenience polyandry”; Hosken and Stockley 2003).

The males in our study population do not lek, and although establishing a territory is related to mating success, most matings do not take place on territories (Moore et al. 1995). Indeed, the locations of matings for males are highly variable, and therefore, mate choice can be distinguished from female preferences for specific locations (Moore et al. 1995; Clutton-Brock and McAuliffe 2009). During the rut, all the males of varying ages and ranks typically join female groups, frequently resulting in aggregations of hundreds of individuals. The males that gain matings usually achieve most of them between 5 and 8 years old (when they are considered “prime-aged”), but they must also attain high social dominance rank at these ages to be able to reproduce (McElligott and Hayden 2000; McElligott et al. 2001, 2002).

We compared precopulatory mate choice in monandrous single-mating females, monandrous multiple-mating females, and polyandrous females to test several potential nonmutually exclusive hypotheses that could help explain the occurrence of polyandry in fallow deer:

- H1. *Fertility insurance hypothesis.* We tested if polyandry could be explained by the fertility insurance hypothesis (Gibson and Jewell 1982). Accordingly, females should remate with a different male if fertilization from the first mating is uncertain. We, therefore, investigated if females were more likely to be polyandrous when their first mating occurred late in the rut or was with a male that had previously achieved high numbers of matings during that day or during the rut. Prime-aged, dominant males achieve high numbers of matings that also tend to

be clustered in time (McElligott and Hayden 2000; Farrell 2001; McElligott et al. 2002), and therefore, sperm depletion is a possibility (Preston et al. 2001).

- H2. *Good genes hypothesis.* We tested if polyandrous females were more likely to mate with males with good/better genes for their second mating. Therefore, females should mate again if their first mates are young and/or low-ranking and if they encounter older, more dominant males than their first mate. Estrus fallow deer females range widely in Phoenix Park and may encounter many males during this period. However, not all males are active at all times, and it is, therefore, possible that females are not with the most preferred male at the time when want to mate (Farrell 2001; Harty 2002). Age and dominance are strongly linked to male reproductive success (McElligott and Hayden 2000; Say et al. 2003; Briefer et al. 2010; Ciuti and Apollonio 2011), and male ability to survive to older ages can reveal superior genes (Brooks and Kemp 2001; McElligott et al. 2002).
- H3. *Offspring quality hypothesis.* We examined if polyandrous females were more likely to produce a viable offspring than monandrous females and if their fawns were larger than those born to monandrous females. Additionally, we tested if multiple-mating monandrous females were more likely to produce a viable offspring, compared to single-mating monandrous females, in order to tease apart the effects of multiple mating versus polyandry on female fitness (Klemme et al. 2007).

Materials and methods

Study site and population

The study was carried out from 1989 to 1998 on a herd of fallow deer in Phoenix Park (709 ha, 80 % pasture, 20 % woodland; 53°22' N, 6°21' W), Dublin, Ireland. The population size varied during the 10-year study, from 470 to 689 individuals. Almost all animals were of known age and individually recognizable, as tagging of the population by the park authorities began in 1971.

Observations during the breeding season

We divided the breeding season into two periods. The prerut refers to the period when males have shed the velvet from their antlers and lasts until the day before the first mating (McElligott et al. 1999). The rut refers to the period when matings occur. During the study, there were 7–13 observers present in the field from dawn until dusk every day (approximately 11 h) during the rut, which ensured maximum coverage of the animals during daylight hours. Matings are generally clustered in time over the course of the day, with

the majority occurring between 11 am and 4 pm and with observation beginning and ending several hours before and after these times, respectively (Farrell 2001). Because we observed a large proportion of the females mating each year, our daytime observations of matings were highly correlated with genetic reproductive success (Farrell 2001; Say et al. 2003). Also, because of occasional monitoring for nighttime mating activity (AGM, personal observation), we know that mating activity during the night is greatly reduced. All event recordings of agonistic interactions and matings were carried out. All observers were in radio contact to facilitate the exchange of information and to prevent duplicate recording of the same behavioral events.

Matings

For each mating, we recorded the following information when possible: identity of the female, identity of the male, and time when ejaculation occurred. Females were considered as single-mating if they mated once during a given fertile period and as multiple-mating if they mated more often than that. Given that estrus can last up to 2 days in fallow deer (Asher et al. 1986), matings of females that had intermating intervals of <50 h were deemed to have mated in the same estrous (Farrell 2001). Matings occurring more than 50 h after a previous mating were not considered because this could suggest that a second estrus may have occurred, with the female not being fertilized during the first one ($N=68$). Matings that occurred <5 min apart were not considered either because they were rare ($N=10$) and always resulted from male sneaking tactics (i.e., male-initiated polyandry rather than female-initiated polyandry; MEF and AGM, personal observations). Females mating with more than one male within their fertile period were considered polyandrous (Birkhead and Møller 1998).

Male dominance relationships

The outcomes of agonistic interactions recorded during the prerut (September and first half of October) were used to calculate dominance ranks for most males between 1989 and 1998 (one measure per male per year, except 1991 and 1992, for which rank data were not available). Male rank is established before the rut so that prerut and rut rank values are highly correlated (McElligott et al. 1999, 2001). The dominance rank of each male was calculated according to the index of Clutton-Brock et al. (1979) and is appropriate for our study (Bang et al. 2010). We used the results of agonistic interactions (wins and losses) to calculate an index of dominance. The male with the highest index value in each year (i.e., the higher-ranking male) was assigned the rank of 1 and all other males were ranked accordingly. We calculated dominance ranks for all males that interacted with at least

10 % of other males. The number of males ranked each year varied between 63 and 75 males.

Fawn size and identification

Fawns were caught in June each year, either by hand or with the help of a small net. To minimize the risk of abandonment, gloves were used when handling fawns and handling time was kept to <15 min (Lord 2006). Hind leg lengths were measured for each individual. This measurement was chosen because it is less prone to error than others and is a good indicator of body size (McElligott et al. 2001). In some cases, we directly observed births. If not, age was estimated using a previously described combination of the degree of hoof hardening, level of umbilical healing, and behavior/hardiness (Lord 2006). Fawns were ear tagged with a unique color and number combination to allow individual identification and then released. Mother–fawn pairs were determined either when mothers were seen with newborns or in July during routine field observations. Suckling events and other contact interactions were used to determine maternity. Both offspring and non-offspring may be involved in suckling events (milk stealing by non-offspring). However, own fawns were identified based on differences in timing of approach to mothers, approach direction, positioning, and maternal behaviors, such as licking and lack of aggression (Birgersson et al. 1991; Lord 2006).

Data analyses

We used 1,552 matings for the analyses, in which the identities of the females were known, varying from 54 matings in 1989 to 231 in 1996 (Table 1). Data on female age ($N=30$ matings without female age), male identity ($N=2$ matings without male

identity), male age ($N=64$ matings without male age), and dominance rank ($N=294$ matings without male rank) were not always available. Ejaculation times, allowing us to calculate the order of matings within a day and the intermating intervals for multiple-mating females, were not available for 14 matings. Data on offspring resulting from 891 matings were available for analyses. When females were observed with a fawn, its sex was known for 307 matings and body measures for 161 matings. As a result, sample sizes varied among the different analyses.

To investigate the fertility insurance hypothesis, the good genes hypothesis, and the offspring quality hypothesis, we used generalized linear mixed model (GLMM) fit by the Laplace approximation and with restricted estimate maximum likelihood (lmer function in R; Bates et al. 2011). This allowed us to test the effect of various factors (e.g., day of the first mating, cumulative number of matings achieved by the male at the time of the mating considered, male age, male dominance rank; Table 2) on (1) the mating pattern adopted by females each year (monandrous, i.e., females that mated with only one male, versus polyandrous, i.e., females that mated with more than one male); (2) the occurrence of females remating with a different male during their estrous period (do not remate with a different male versus remate with a different male); (3) the order in which males were chosen by polyandrous females (chosen first versus chosen second; the third or fourth males chosen were disregarded in these analyses, as they represented a very small minority of the matings; 14 out of 351 matings by polyandrous females); (4) the occurrence of females being observed with fawns (observed with fawn versus observed without fawn; females that were not observed were not considered in these analyses); and (5) fawn hind leg length. We fit the sets of models 1 to 4 with a binomial family distribution and logit link function and model 5 with a Gaussian family distribution and

Table 1 Data used in the analyses

Year	Matings	Females	Single-mating females	Multiple-mating females	Percent	Polyandrous females	Percent
1989	54	49	45	4	8.2	3	6.1
1990	57	54	51	3	5.6	3	5.6
1991	158	139	120	19	13.7	14	10.1
1992	109	91	75	16	17.6	10	11.0
1993	140	124	110	14	11.3	10	8.1
1994	202	163	128	35	21.5	30	18.4
1995	179	162	146	16	9.9	15	9.3
1996	231	185	144	41	22.2	37	20.0
1997	220	181	147	34	18.8	31	17.1
1998	202	167	138	29	17.4	26	15.6
Total	1,552	1,316	1,104	211		179	

Number of matings, number of females involved in the matings, number of single-mating females, number and percentage of multiple-mating females, and number and percentage of polyandrous females for each year of the study. Single-mating females mated only once; multiple-mating females mated several times with the same male or different males during a given fertile period; polyandrous females mated with more than one male during a given fertile period

Table 2 Models fit to investigate the various polyandry hypotheses

Response variable	Model	Hypothesis	Fixed effect(s)	<i>z</i>	<i>P</i>	Sample size	Random effects
1. Polyandrous/monandrous	1	Fertility insurance	Day	0.44	0.66	1,290	Female ID+Year
2. Occurrence of females remating with a different male	2	Fertility insurance	Male daily matings	0.61	0.54	1,166	Female ID+Male ID+Year
	3	<i>Fertility insurance</i>	<i>Male rut matings</i>	2.72	0.006		
	4	<i>Good genes</i>	<i>Male age</i>	2.03	0.042		
	5	Good genes	Male rank	−0.29	0.77		
3. Order in which males were chosen by polyandrous females	6	Good genes	Male age	−0.31	0.76	286	Female ID+Male ID+Year
	7	Good genes	Male rank	1.27	0.21		
4. Occurrence of females with fawns	8	Offspring quality	Multiple-mating/ single-mating	0.79	0.43	763	Female ID+Year
	9	Offspring quality	Polyandrous/monandrous	1.07	0.29		
5. Fawn hind leg length	10	Offspring quality	Polyandrous/monandrous	−0.33	0.74	100	Female ID+Year

The response variable and fixed and random effects included in the models as well as the sample size (number of matings) are indicated. Significant results are in italics. Single-mating females mated only once; multiple-mating females mated several times with the same male or different males during a given fertile period; polyandrous females mated with more than one male during a given fertile period

Day day of the first mating, *Male daily/rut matings* cumulative number of matings achieved daily/during the rut by the male at the time of the mating considered, *Female/Male ID* female/male identity

identity link function, after ensuring that the residuals followed a normal distribution (Wu 2009). In these models, female identity, male identity (when necessary), and the year of observation were included as random effects to control for repeated measurements of the same individuals within and between years and for potential between-year differences (Table 2). For each set of models, we added female age as a control factor if this term had a significant effect on the dependent variable (i.e., for model 4: $z=-2.10$, $p=0.036$; for model 5: $z=4.06$, $p<0.0001$). When testing for the effect of female age, male age, male dominance rank, day of the first mating, and cumulative number of matings achieved daily/during the rut by the male at the time of the mating considered, we added as a control factor the sample size for each category of age, rank, day, or number of matings. This accounted for the potential effect of the differences in sample sizes between categories on the proportion of polyandrous females (model 1), the proportion of females remating with another male (models 2), or the proportion of males chosen first or second (model 3). Finally, in model 4, fawn age and fawn sex were also included as controls.

In addition, when our analyses revealed several models within a set that were significant, we applied Akaike's information criterion (AIC) adjusted for small sample size (AIC_C ; Burnham and Anderson 2002) to identify the model that best explained the variation in the dependent variable (Table 2). We used AIC_C despite the large sample size in our data because AIC_C converges to AIC as sample size increases and should be used by default (Burnham et al. 2011; Symonds and Moussalli 2011). To allow this model selection, each set of models was carried out on the same data because AIC cannot be compared between models carried out on different datasets (Symonds and Moussalli 2011).

Therefore, for example, to test both the effect of the cumulative numbers of matings achieved daily by males at the time of the matings considered and of male age and dominance rank on the occurrence of females remating with a different male, only data in which the number of matings achieved, male age, and male rank were known were considered (Table 2). AIC_C was calculated from models fit with maximum likelihood, and the models to compare included the same control factors. When the difference between the AIC_C values of two models (ΔAIC_C) is <2 units, both models have support and can be considered competitive. Models with ΔAIC_C ranging from 3 to 7 have considerably less support by the data, models with $\Delta AIC_C >10$ are poorly supported, and $\Delta AIC_C >20$ have no empirical support (Burnham and Anderson 2002; Burnham et al. 2011). Akaike weights (w_i) indicate the probability that a particular model is supported by the data among those included in the set of candidate models (Burnham and Anderson 2002). For each model, we also calculated the evidence ratio, defined as the ratio between the Akaike weight of the best model and the Akaike weights of the competing model, to determine to what extent it is better than another.

We carried out statistical analyses using R v.2.15.0. All tests were two-tailed and results retained significance when $P<0.05$. All means are given with standard errors (SEs).

Results

Proportion of multiple-mating and polyandrous females and intermating intervals

Mating females were aged 1–23 years old, and mating males were aged 2–9 years old (Table S1). Males older than 9 years old

were excluded from mating due to competition from others (McElligott and Hayden 2000). The vast majority of matings (96.5 %) were by males aged 5–8 years old (Table S1). Over the study period, females ($N=469$ individuals in total) were present and observed mating for 1–9 years (2.8 ± 0.1 years) and males ($N=113$ individuals in total) for 1–5 years (1.7 ± 0.1 years). Each year, on average, 14.6 ± 1.8 % of all females ($N=10$ years) mated more than once with the same male or different males (multiple-mating and polyandrous females) and 12.1 ± 1.7 % of all females mated with more than one male during a fertile period (polyandrous females; Table 1). The majority of multiple-mating females mated twice (89.1 %, $N=188/211$ females), and the majority of polyandrous females mated with two different males (92.7 %, $N=166/179$ females). Some females mated three times ($N=21/211$ females) and with three different males ($N=11/179$ females). One female was recorded mating four times and another one six times with four different males. In total, 19.0 % of the multiple-mating females ($N=40/211$ females) mated at least twice with the same male. Females that mated multiply during an estrus did so for 1.29 ± 0.04 years (range, 1–3 years) over the 10-year study. The mean intermating interval for multiple-mating females was 6.11 ± 0.54 h ($N=224$ intervals; range, 0.11–49.86 h).

Fertility insurance hypothesis

Females were not more likely to be polyandrous if their first mating occurred towards the end of the rut, compared to earlier, independently of their age (Table 2, model 1). Females were also not more likely to remate with a different male when their current mate had previously achieved high numbers of matings during the day (Table 2, model 4). However, females were more likely to remate with a different

male when their current mate had previously achieved high numbers of matings during the rut (GLMM; Table 2, model 3; Fig. 1).

Good genes hypothesis

Females that mated with relatively older males were more likely to remate with a different male (Table 2, model 4; Fig. 2). The small number of females mating with 3- to 4-year-old males were not polyandrous ($N=14$ matings). The proportion of females remating with a different male was not affected by male dominance rank (GLMM; Table 2, model 5). Neither age (Table 2, model 6) nor dominance rank of males (Table 2, model 7) influenced the order in which males were selected for mating by polyandrous females.

Offspring quality hypothesis

Multiple-mating females (Table 2, model 8) and polyandrous females (Table 2, model 9) were not more likely to be observed with a fawn during the following year compared to other females. Further, the size of polyandrous females' fawns was not different to the size of monandrous females' fawns, independently of fawn's sex and estimated age (Table 2, model 10).

Model selection

Our analyses revealed two models (3 and 4) within the same set (2) that were significant (Table 2). Polyandry was related to male rut matings (model 3) and male age (model 4). We thus compared these models using AIC_C . This model selection procedure selected model 3 (male rut matings; $AIC_C=$

Fig. 1 Relationship between the cumulative numbers of matings achieved by males during the rut at the time of the matings considered and the proportion of females remating with a different male (model residuals controlled for the sample size for each category of numbers of matings (1 to 107 matings); mean \pm SE). Females were more likely to remate with a different male when their current mate had previously achieved high numbers of matings during the rut

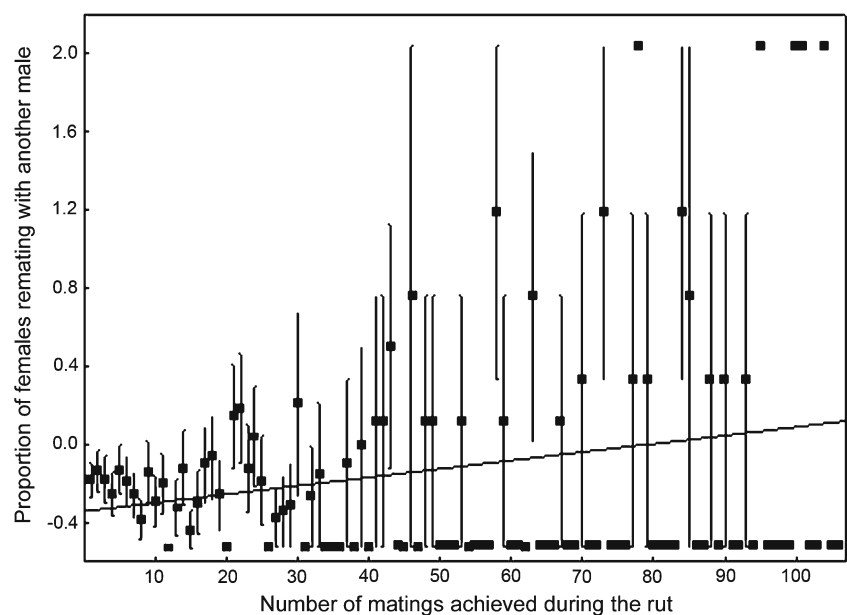
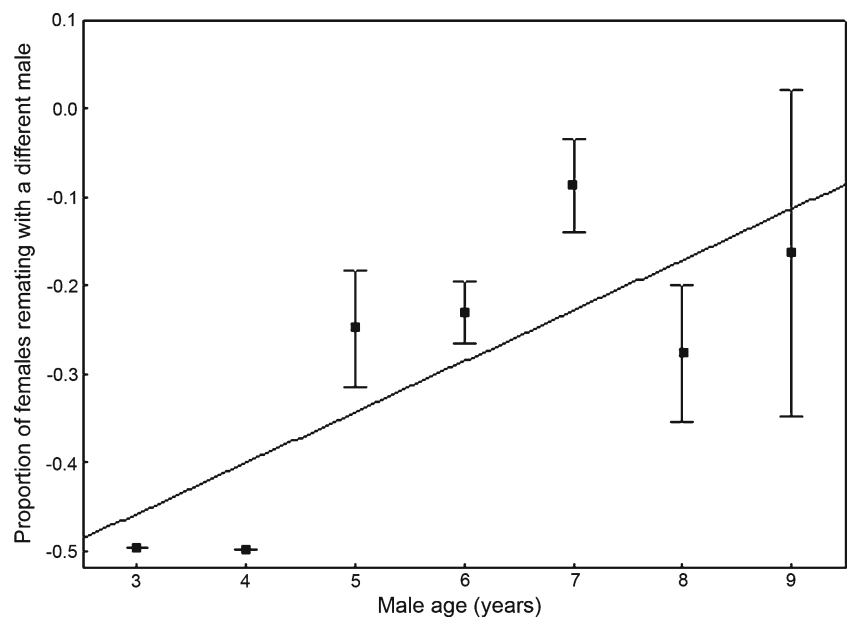


Fig. 2 Relationship between male age and the proportion of females remating with a different male (model residuals controlled for the sample size for each category of male age (3–9 years old); mean \pm SE). A higher proportion of females mating with older males (5–9 years old) remated with a different male afterwards, compared to females mating with relatively younger males (3–4 years old). None of the females mating with 3- to 4-year-old males remated with a different male afterwards ($N=14$ matings)



903.01) over model 4 (male age; $AIC_C=905.87$). Both models were competitive ($\Delta AIC_C=2.87$), but model 3 had 81 % chance ($w_i=0.81$; $ER=1.00$) to be the best model, compared to model 4. Thus, the cumulative numbers of matings achieved during the rut by males at the time of the matings considered were a better predictor than male age in explaining the occurrence of females remating with a different male.

Discussion

Using a long-term dataset, we examined the potential benefits of polyandry, by comparing monandrous single-mating, monandrous multiple-mating, and polyandrous female fallow deer. The female fitness benefits of polyandry have rarely been tested in wild mammal populations (but see Fisher et al. 2006; Bergeron et al. 2011) and particularly for large, monotocous ungulates. We found that, on average, 12 % of females were polyandrous each year. This small but consistent proportion of polyandrous females suggests that monandry and polyandry are alternative female strategies. The likelihood of females mating with different males was affected by two male factors: the cumulative number of matings achieved during the rut by the male at the time of the mating considered, and male age. In accordance with the fertility insurance hypothesis and contrary to the good genes hypothesis, females were more likely to remate with a different male when their first mate had previously achieved a high number of matings during the rut or was relatively old and, therefore, potentially at risk of sperm depletion (Preston et al. 2001). Furthermore, our model selection indicated that the numbers of matings achieved by males during the rut was a better predictor than male age for the likelihood of females remating. Therefore, the evidence points to

polyandry in fallow deer being linked to female fertilization probability because of the potential risks of male sperm depletion. Our results underline the importance of considering female reproductive strategies in polygynous mammals. These strategies are likely to involve complex trade-offs between fertilization success, preferences for high-quality males, and the potential costs of polyandry for monotocous species (Preston et al. 2001; Carranza et al. 2009).

Our results show that females were not more likely to be polyandrous when their first mating occurred towards the end of the rut or when their first mate had previously achieved high numbers of matings during the day. However, they were more likely to be polyandrous when their first mate had previously achieved high numbers of matings during the rut. This could be related to sperm depletion and longer-term, overall loss of condition during the course of the rut (McElligott et al. 2003; Vannoni and McElligott 2009). In feral sheep (*Ovis aries*), dominant males that mated often (13 times per day) became sperm-depleted, resulting in fewer fertilizations (Preston et al. 2001). In red deer (*Cervus elaphus*), only males with high testosterone levels might be partially able to counteract the effect of sperm depletion, by producing better-quality sperm (Malo et al. 2009). The overall number of matings achieved during the rut may be a better indicator of sperm depletion than the number of matings achieved during the day, which could explain why we did not find a relationship between the proportion of females remating and the number of daily matings.

According to the good genes hypothesis, females should remate with an older and/or more dominant male when their first mating was with a young (e.g., 2–4 years old) and/or low-ranking male (e.g., rank >10). Our results showed that neither male age nor dominance rank influenced the order in which they were selected for matings by polyandrous females.

Furthermore, the dominance rank of males did not influence the likelihood of females remating with a different male. However, contrary to what we predicted, females mating with relatively older males (5–9 years old) were more likely to remate with a different male, compared to females mating with younger males (3–4 years old). In our study population, most matings are gained by dominant, prime-aged males (McElligott and Hayden 2000; McElligott et al. 2002), and there is robust evidence that these have higher phenotypic quality (i.e., higher survival rates and more likely to mate again during subsequent rut; McElligott et al. 2002; Say et al. 2003). Female fallow deer do not prefer young males; they avoid mating with 2.5-year-old males and delay estrous even when there are costs associated with weight loss and delayed reproduction (Komers et al. 1999). However, our results suggest that, despite the small number of matings ($N=14$) achieved by these 3- to 4-year-old males, these females were not polyandrous. Similarly, Stopher et al. (2011) found that red deer hinds in estrus that changed harems were more likely to enter the harems of younger males. Old males get more matings than young males (McElligott et al. 2002) and, as a result, are more likely to be subject to daily or seasonal sperm depletion (Preston et al. 2001). They could also accumulate more deleterious mutations in the germ line and have lower fertilization success (Johnson and Gemmell 2012). An assessment of the quantity and quality of sperm produced by fallow bucks at different ages would be required to fully understand why the females mating with relatively younger males were not polyandrous.

Our results suggest that polyandrous females did not have higher-quality offspring (more viable and larger fawns) than other females. Polyandrous and monandrous multiple-mating females were not more likely than single-mating females to be observed with a fawn during the following year. Polyandrous females also did not have larger fawns than monandrous females. These findings contrast with those for roe deer (*Capreolus capreolus*, in which twinning is common), showing that polyandry increases offspring viability and quality (Madsen et al. 1992; Vanpé et al. 2009). However, unlike most other species studied, the most dimorphic ungulates are usually monotocous (Bro-Jørgensen 2011). Our evidence points to fallow deer females being polyandrous when their first mating was potentially unsuccessful and, therefore, in order to increase the likelihood of producing a viable offspring the following year. As a result, offspring quality was similar in polyandrous and monandrous females.

To conclude, polyandry in fallow deer is likely to be best explained by the fertility insurance hypothesis. Female reproductive strategies involve complex trade-offs between fertility success, preferences for high-quality males, and potential costs of polyandry (Preston et al. 2001; Bro-Jørgensen 2011). Offspring quality would potentially be higher if females mated with high-quality males. However, if high-quality males become sperm-depleted, females may need to

remate with lower-quality ones to ensure fertilization, thereby ensuring births during the optimal period the following year. The potential for different female mating strategies in polygynous mammals has often been overlooked. We hope that this detailed examination of fallow deer polyandry will stimulate interest in this phenomenon for other species.

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Ethical standards The work described here complies with the current laws of Ireland.

Conflict of interest The authors declare that they have no conflict of interest.

References

- Andersson M (1994) Sexual selection. Princeton University Press, Princeton
- Asher GW, Barrell GK, Peterson AJ (1986) Hormonal changes around oestrus of farmed fallow deer, *Dama dama*. J Reprod Fert 78:487–496
- Bang A, Deshpande S, Sumana A, Gadagkar R (2010) Choosing an appropriate index to construct dominance hierarchies in animal societies: a comparison of three indices. Anim Behav 79:631–636
- Bates D, Maechler M, Bolker B (2011) lme4: linear mixed-effects models using Eigen and Eigen. R package version 2.15.0. Available at <http://CRAN.R-project.org/package=lme4>.
- Bebíé N, McElligott AG (2006) Female aggression in red deer (*Cervus elaphus*): does it indicate competition for mates? Mamm Biol 71:347–355
- Bergeron P, Réale D, Humphries MM, Garant D (2011) Evidence of multiple paternity and mate selection for inbreeding avoidance in wild eastern chipmunks. J Evol Biol 24:1685–1694
- Birgesson B (1998) Male-biased maternal expenditure and associated costs in fallow deer. Behav Ecol Sociobiol 43:87–93
- Birgesson B, Ekvall K, Temrin H (1991) Allosuckling in fallow deer, *Dama dama*. Anim Behav 42:326–327
- Birkhead TR, Møller AP (1998) Sperm competition and sexual selection. Academic, London
- Bowyer R, Rachlow J, Stewart K, Van Ballenberghe V (2011) Vocalizations by Alaskan moose: female incitation of male aggression. Behav Ecol Sociobiol 65:2251–2260
- Briefer E, Vannoni E, McElligott AG (2010) Quality prevails over identity in the sexually selected vocalisations of an ageing mammal. BMC Biol 8:35
- Bro-Jørgensen J (2002) Overt female mate competition and preference for central males in a lekking antelope. P Natl Acad Sci USA 99:9290–9293
- Bro-Jørgensen J (2007) Reversed sexual conflict in a promiscuous antelope. Curr Biol 17:2157–2161
- Bro-Jørgensen J (2011) Intra- and intersexual conflicts and cooperation in the evolution of mating strategies: lessons learnt from ungulates. Evol Biol 38:28–41

- Brooks R, Kemp DJ (2001) Can older males deliver the good genes? *Trends Ecol Evol* 16:308–313
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York
- Burnham KP, Anderson DR, Huyvaert KP (2011) AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behav Ecol Sociobiol* 65:23–35
- Byers JA, Waits L (2006) Good genes sexual selection in nature. *P Natl Acad Sci USA* 103:16343–16345
- Byers JA, Wiseman PA, Jones L, Roffe TJ (2005) A large cost of female mate sampling in pronghorn. *Am Nat* 166:661–668
- Carling MD, Avsharian Wiseman P, Byers JA (2003) Microsatellite analysis reveals multiple paternity in a population of wild pronghorn antelopes (*Antilocapra americana*). *J Mammal* 84:1237–1243
- Carranza J, Pérez-González J, Mateos C, Fernández-García JL (2009) Parents' genetic dissimilarity and offspring sex in a polygynous mammal. *Mol Ecol* 18:4964–4973
- Ciuti S, Apollonio, M (2011) Do antlers honestly advertise the phenotypic quality of fallow buck (*Dama dama*) in a lekking population? *Ethology* 117:133–144
- Clutton-Brock TH, McAuliffe K (2009) Female mate choice in mammals. *Q Rev Biol* 84:3–27
- Clutton-Brock TH, Albon SD, Gibson RM, Guinness FE (1979) The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus* L.). *Anim Behav* 27:211–225
- Collet J, Richardson DS, Worley K, Pizzari T (2012) Sexual selection and the differential effect of polyandry. *P Natl Acad Sci USA* 109:8641–8645
- Cornell SJ, Tregenza T (2007) A new theory for the evolution of polyandry as a means of inbreeding avoidance. *Proc R Soc Lond B* 274:2873–2879
- Daly M (1978) The cost of mating. *Am Nat* 112:771–774
- Dunn SJ, Clancey E, Waits LP, Byers JA (2012) Genetic evidence of inbreeding avoidance in pronghorn. *J Zool* 288:119–126
- Endo A, Doi T (2002) Multiple copulations and post-copulatory guarding in a free-living population of sika deer (*Cervus nippon*). *Ethology* 108:739–747
- Farrell ME (2001) Courtship, multiple mating and reproductive synchrony in female fallow deer (*Dama dama*). Ph.D. thesis, University College Dublin, Dublin.
- Farrell ME, Briefer E, Hayden T, McElligott AG (2011) Assortative mating in fallow deer reduces the strength of sexual selection. *PLoS One* 6:e18533
- Fedorka KM, Mousseau TA (2002) Material and genetic benefits of female multiple mating and polyandry. *Anim Behav* 64:361–367
- Firman RC, Simmons LW (2011) Male house mice evolving with post-copulatory sexual selection sire embryos with increased viability. *Ecol Lett* 15:42–46
- Fisher DO, Double MC, Blomberg SP, Jennions MD, Cockburn A (2006) Post-mating sexual selection increases lifetime fitness of polyandrous females in the wild. *Nature* 444:89–92
- Gibson RM, Jewell PA (1982) Semen quality, female choice and multiple mating in domestic sheep: a test of Trivers' sexual competence hypothesis. *Behaviour* 80:9–31
- Harty HC (2002) Mate selection by females: sampling tactics and mate choice by female fallow deer (*Dama dama* L.). Ph.D. thesis, University College Dublin, Dublin
- Hosken DJ, Stockley P (2003) Benefits of polyandry: a life history perspective. *Evol Biol* 33:173–194
- Huchard E, Canale CI, Le Gros C, Perret M, Henry P-Y, Kappeler PM (2012) Convenience polyandry or convenience polygyny? Costly sex under female control in a promiscuous primate. *Proc R Soc Lond B* 279:1371–1379
- Jennions MD, Petrie M (2000) Why do females mate multiply? A review of the genetic benefits. *Biol Rev* 75:21–64
- Johnson SL, Gemmell NJ (2012) Are old males still good males and can females tell the difference? *Bioessays* 34:609–619
- Klemme I, Eccard JA, Ylönen H (2007) Why do female bank voles, *Clethrionomys glareolus*, mate multiply? *Anim Behav* 73:623–628
- Komers PE, Birgersson B, Ekvall K (1999) Timing of estrus in fallow deer is adjusted to the age of available mates. *Am Nat* 153:431–436
- Langbein J, Putman R (1992) Reproductive success of female fallow deer in relation to age and condition. In: Brown RD (ed) *The biology of deer*. Springer, New York, pp 293–299
- Lord M (2006) Neonatal and maternal behaviour in fallow deer (*Dama dama* L.). Ph.D. thesis, University College Dublin, Dublin
- Madsen T, Shine R, Loman J, Hakansson T (1992) Why do female adders copulate so frequently? *Nature* 335:440–441
- Malo A, Roldan ER, Garde J, Soler A, Vicente J, Gortazar C, Gomendio M (2009) What does testosterone do for red deer males? *Proc R Soc Lond B* 276:971–980
- McElligott AG, Hayden TJ (2000) Lifetime mating success, sexual selection and life history of fallow bucks (*Dama dama*). *Behav Ecol Sociobiol* 48:203–210
- McElligott AG, O'Neill KP, Hayden TJ (1999) Cumulative long-term investment in vocalization and mating success of fallow bucks, *Dama dama*. *Anim Behav* 57:1159–1116
- McElligott AG, Gammell MP, Harty HC, Paini DR, Murphy DT, Walsh JT, Hayden TJ (2001) Sexual size dimorphism in fallow deer (*Dama dama*): do larger, heavier males gain greater mating success? *Behav Ecol Sociobiol* 49:266–272
- McElligott AG, Altwegg R, Hayden TJ (2002) Age-specific survival and reproductive probabilities: evidence for senescence in male fallow deer (*Dama dama*). *Proc R Soc Lond B* 269:1129–1137
- McElligott AG, Naulty F, Clarke W, Hayden TJ (2003) The somatic cost of reproduction: what determines reproductive effort in prime-aged fallow bucks? *Evol Ecol Res* 5:1239–1250
- Moore N, Kelly P, Cahill J, Hayden T (1995) Mating strategies and mating success of fallow (*Dama dama*) bucks in a non-lekking population. *Behav Ecol Sociobiol* 36:91–100
- Pischedda A, Rice WR (2012) Partitioning sexual selection into its mating success and fertilization success components. *P Natl Acad Sci USA* 109:2049–2053
- Preston BT, Stevenson IR, Pemberton JM, Wilson K (2001) Dominant rams lose out by sperm depletion. *Nature* 409:681–682
- Say L, Naulty F, Hayden TJ (2003) Genetic and behavioural estimates of reproductive skew in male fallow deer. *Mol Ecol* 12:2793–2800
- Slatyer RA, Mautz BS, Backwell PRY, Jennions MD (2012) Estimating genetic benefits of polyandry from experimental studies: a meta-analysis. *Biol Rev* 87:1–33
- Stopher KV, Nussey DH, Clutton-Brock TH, Guinness F, Morris A, Pemberton JM (2011) The red deer rut revisited: female excursions but no evidence females move to mate with preferred males. *Behav Ecol* 22:808–818
- Symonds MRE, Moussalli A (2011) A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behav Ecol Sociobiol* 65:13–21
- Tregenza T, Wedell N (2002) Polyandrous females avoid costs of inbreeding. *Nature* 415:71–73
- Vannoni E, McElligott AG (2009) Fallow bucks get hoarse: vocal fatigue as a possible signal to conspecifics. *Anim Behav* 78:3–10
- Vanpé C, Kjellander P, Gaillard JM, Cosson JF, Galan M, Hewison AJM (2009) Multiple paternity occurs with low frequency in the territorial roe deer, *Capreolus capreolus*. *Biol J Linn Soc* 97:128–139
- Wolff JO, Macdonald DW (2004) Promiscuous females protect their offspring. *Trends Ecol Evol* 19:127–134
- Wu L (2009) Mixed effects models for complex data. Chapman and Hall, Boca Raton
- Yasui Y (1998) The "genetic benefits" of female multiple mating reconsidered. *Trends Ecol Evol* 13:246–250